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Seasonal fluctuation and mortality schedule for immatures of *Hypna clytemnestra* (Butler), an uncommon neotropical butterfly (Nymphalidae: Charaxinae)

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Abstract. I describe the pattern of abundance and a mortality schedule for a population of *Hypna clytemnestra huebneri* (Butler) (Nymphalidae: Charaxinae), an uncommon neotropical butterfly inhabiting southeastern Brazil. Over a one year period I gathered data on the abundance of immatures through periodic censuses on 65 host plants, whereas adults were trapped monthly. A marked seasonal variation in abundance of immatures was detected, with a peak during the wet season. Adults were present throughout the year, but at very low numbers. The construction of a life-table showed that the main mortality factors acting upon immatures were parasitoids and predators. Eggs and medium to large-sized larvae suffered higher mortality, characterizing a mixed Type II/III survivorship curve. The data highlight the effect of predators upon larval stage as well as the great impact of parasitoids on eggs, which contrasts to the usually low intensity of egg parasitism reported for temperate species. These results reinforce general trends detected in recent literature reviews for more abundant and/or pest species towards the importance of natural enemies as mortality factors of herbivorous insects.

Key words: *Hypna*, life-table, parasitism, predation, seasonality, survivorship curve.

INTRODUCTION

To achieve a fuller understanding of the processes and factors governing fluctuations of animal populations, an important first step consists of describing these fluctuations in the field at different time-scales, including species with different life-histories inhabiting different habitats and showing different patterns of abundance. The increase in the number of descriptive studies in different ecological contexts may lead to the detection of hidden patterns (Price, 1991) and make possible the establishment of more comprehensive and reliable generalizations (e.g. Cornell & Hawkins 1995; Hawkins et al. 1997; Cornell et al. 1998).

For temperate regions many of studies on demography of herbivorous insects are already available, encompassing several different groups. The order Lepidoptera is relatively well represented, although many studies refer to very abundant and/or pest species (reviews in Dempster 1983; Courtney 1986; Cornell & Hawkins 1995; Hawkins et al. 1997; Cornell et al. 1998). Yet, for neotropical region, despite the increasing number of studies on population dynamics of adult butterflies (e.g. Ehrlich & Gilbert 1973; Vasconcellos-Neto 1980; Saalfeld & Araújo 1981; Quintero 1988; Freitas 1993, 1996; Ramos & Freitas 1999, Vanini et al. 2000; Freitas & Ramos 2001, Freitas et al. 2001), field investigations on immature populations of Lepidoptera in natural habitats are still scarce. This is especially true for investigations employing life-table methods, of which the few examples include the studies of Costa (1991) on the butterfly *Hypothyris* *ninonia daeta* (Bdv.) and Caldas (1995a,b, 1996), dealing with the populational dynamics of the juvenile stages of *Anaea ryphea* (Cramer) in southeastern Brazil and in Panama. This paucity of data on mortality schedules for immature stages of neotropical Lepidoptera inhabiting natural systems is even more striking for uncommon species.

In a population study of the butterfly *Pieris virginiensis* Edwards, Cappuccino & Kareiva (1985) correctly argued that because in natural habitats most insect species are rare, the understanding of the relationships between these species and their host plants is essential to any theory of plant-insect interaction. Besides that, the greater emphasis put in studies of very abundant or of economic value species could lead us to biased generalizations (Hayes 1984; Hawkins et al. 1997). In a review on novel approaches to studies of population dynamics, Cappuccino (1995) called for more studies of rare species, in spite of the obvious difficulties of data gathering in these cases due to the low population sizes. If we want to get a broader and unbiased picture of mortality patterns for herbivorous insects, it is clear that more quantitative descriptive studies are needed.

In this study I describe the seasonal abundance fluctuation and mortality schedule for immature stages (eggs and larvae) of a population of the butterfly *Hypna clytemnestra huebneri* (Butler), a widely distributed but locally uncommon charaxine (Nymphalidae) inhabiting southeastern Brazil.

MATERIAL AND METHODS

Study organisms

Hypna clytemnestra (Butler 1866) is a medium-sized (forewing length 40-45 mm), relatively cryptic butterfly. A general description of the species can be found in Comstock (1961). In the study area females lay eggs singly on the underside of leaves of *Croton floribundus* Spreng (Euphorbiaceae), a latescent pioneering plant commonly found in the reserve. This species is also used as host plant by another Charaxinae butterfly, *Anaea ryphea*, which is very abundant in the area (Caldas 1994, 1995a) and occasionally by *A. appias* (Hübner), *A. otrere* (Hübner) and possibly *A. arginussa* (Geyer). Individuals of *C. floribundus* of varying sizes, from seedlings to saplings or trees are found in both sunny and shady areas, isolated or in patches, mostly along the trails or on the borders of the forest. Leaves vary in size (10 to 20 cm) depending on the height of plants. During the dry season plants tend to dry out, with a reduction in the production of new leaves and in their nutritional quality (unpublished data).

Younger larvae (first to third instars) construct frass-chains (pers. obs.) which are used during the whole larval period. Larvae are sedentary, staying on the frass chains most of the time, leaving these sites only to feed during short bouts. Fifth instar larvae leave the host plants to pupate. Adults sometimes fly along sunny trails and forest gaps, but during mid-day males usually perch on sunny sites along trails, displaying territorial behavior. Like other Charaxinae, they feed on rotten fruits, carrion and feces (Young 1982; DeVries 1987).

Study site

The study was carried out at the Reserva de Santa Genebra, located at Campinas (22° 44' S, 47° 06' W, elevation 670 m), state of São Paulo, Brazil. The reserve is a 251,7 ha patch of disturbed subtropical semideciduous moist forest, surrounded by crops of corn and soybeans, and other human infrastructures. Mean monthly temperature varies from 18°C to 29°C, with daily fluctuations of as much as 20°C from July to September (Morellato & Leitão-Filho 1995). There is a dry season from April to August, characterized by low temperatures and low precipitation, followed by a warmer and wet season, from September to May (Fig. 1).

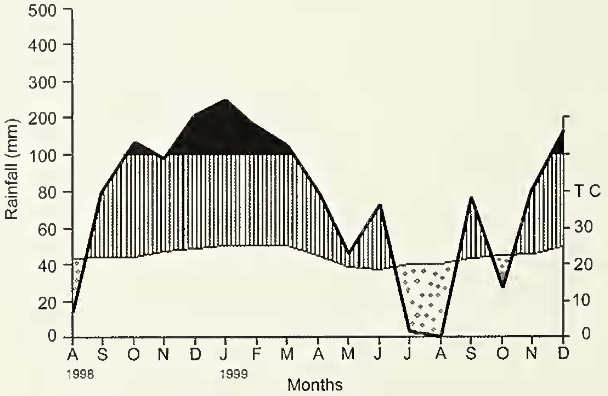

Fig. 1. Climatic diagram of the Reserva de Santa Genebra region during the study period (November1998 - December1999). Hatched = humid period, black = superhumid period and dotted = dry period (following Walter, 1985).

Mortality pattern of *Hypna clytemnestra* population

To investigate the abundance and mortality pattern of *H. clytemnestra* immatures, from November 1998 to November 1999 I inspected 65 previously tagged plants of a population of *C. floribundus* for the presence of eggs and larvae. They were inspected at three-day intervals from early to mid-season, and once a weak from February on. All tagged plants were distributed along the edges of a 1,160 m central trail which passes through the area. I individualized eggs and larvae through a combination of India ink markings on leaf limb and plastic rings placed around leaf petiole. These procedures permitted recordings of immature numbers and positions on each leaf and on each individual plant, making it possible to track their development and survivorship (cf. Caldas 1995a). Eggs and larvae that disappeared between two consecutive inspections were assumed as have been preyed upon.

I constructed a multiple decrement life-table (Carey 1993), which permits identification of the stages of life suffering the highest mortality as well as evaluation of the effect of different mortality factors acting simultaneously. I carried out a competing risk analysis (Carey 1993), a mathematical approximation that permits inference of the effect of one cause of mortality when another cause that occurs simultaneously is eliminated. In this method, if we have two causes of mortality, A and B, q_A is the proportion of individuals inferred to die when cause B is absent, and q_B is the proportion of individuals inferred to die if cause A is absent. D_A and D_B denote the fraction of all individuals observed to die from cause A and B, respectively. Then q_A can be found by solving the equation:

$$aq_A^2 + bq_A + c = 0$$

where

$a = D_A$ $\quad\quad$ $+ = -(D_A + D_B)$

$c = D_B(D_A + D_B)$ $\quad\quad$ $q_B = q_A D_B / D_A$

For a detailed explanation and rationale of the method see Carey (1993: 26-29).

To evaluate the variation in adult abundance of *H. clytemnestra* I employed 12 traps (p. 35 in DeVries 1987) baited with fermented bananas, distributed as follows: four traps on the forest edges, four traps along the central trail (study trail), and four traps inside the forest. Forest edges were characterized by an abrupt transition between forest and open fields with crop vegetation. Traps on the central trail were in the middle of the forest, but in a kind of habitat looking like a gap, due to the relatively open canopy and more intense light penetration, whereas traps inside the forest were in a more humid and shady environment. Traps were hung 1.5 to 3.5 m above the ground. Each sampling consisted of opening traps around noon and closing them the following day at the same time. Captured butterflies were individually marked on the hindwing with a felt-tipped pen and then released. I took four samples each month, from March 1999 to February 2000, totaling 48 samplings.

RESULTS

The population of *H. clytemnestra* showed a seasonal pattern of abundance fluctuation for the immature stages not seen in the adults (Fig. 2). The number of eggs and larvae increased from a very low level in late November/early December 1998 to a peak in late January/early March. This peak was then followed by a sudden reduction in number of immatures to reach the level observed at the beginning of the growing season. During the rest

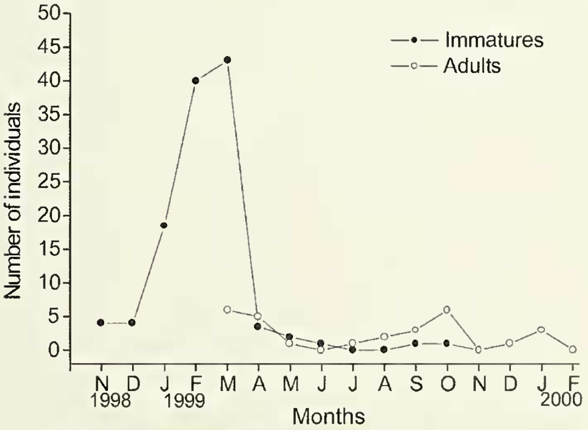

Fig. 2. Abundance fluctuation of immatures and adults of *Hypna clytemnestra* at the Reserva de Santa Genebra, Campinas, SP, from November/1998 to February/2000.

of the year just a few immatures (less than 5) or even none (in the dry season) were recorded on the host plant population.

The number of adults trapped monthly was consistently low (0 to 6), resulting in a total of only 28 individuals captured (as a comparison, at the same period 419 individuals of the abundant species *A. ryphea* were trapped). No clear peak in adult abundance was detected (Fig. 2). The captured individuals were not uniformly distributed among habitats ($X^2 = 8.85$; df = 2; p = 0.012). Most were captured on the central trail (50.0%) and inside the forest (42.9%), while few were trapped on the forest edge (7.1%). Only four individuals were recaptured, with the following recorded residence times (i.e., time elapsed between capture and last recapture): 3, 18, 23 and 36 days. It should be noted that despite the extremely low abundance, adults were trapped even during the dry season months.

In all, 211 immatures were followed from egg to death. The egg stage suffered highest mortality (ca. 80.0%), attributed to both parasitism and predation (Table 1, Fig. 3). Despite this intense mortality, I did not directly observe predation on eggs or larvae of any instar during censuses, though on two occasions I observed eggs being parasitized. Although these eggs are very small, they can be readily seen with the naked eye after one gets used to the contrast between leaf surface and egg color. Several events of egg parasitism were also observed for eggs of the butterfly *A. ryphea* on the same plants.

Eggs of *H. clytemnestra* were parasitized by an Eulophidae species. Mortality of first and second instars were less intense (7.0 and 22.5%, respectively) than those of third and fourth instars (54.8 and 64.3%). Only 2.3% of the eggs reached fifth instar. Mortality of the fifth instar larvae could not be estimated since larvae in this phase of development leave the plants to pupate. All larval mortality was attributed to predation. Even if we assume mortality factors acting upon fifth instar larvae and pupae to be negligible (which is unlikely) the percentage of immatures actually reaching adulthood is less than 2.3%.

Thus, eggs and medium to large-sized larvae were the stages with greatest risk of mortality (Table 1). Even correcting for differences in stage/instar duration by considering probability of survival on a daily basis, this pattern of mortality did not change, indicating that the tendency for more intense mortality of eggs and larger larvae was not an artifact due to differences in amount of time exposed to natural enemies (see values inside parenthesis in the first column of Table 1). Therefore the intensity of mortality suffered by eggs and all larval instars considering the whole season generates a mixed survivorship curve of Types II/III, based on Deevey´s (1947) general classification (Fig. 3).

The competing risk analysis for eggs showed that if predation was eliminated as a cause of mortality, egg parasitism alone would kill 58.1% of the eggs, instead of the 42.6% actually killed. If parasitism

Table 1. The multiple decrement life-table for immature stages of a population of the butterfly *Hypna clytemnestra* studied during 1998/1999 at the Reserva de Santa Genebra, Campinas, SP, Brazil.

Stage ¹	Number beginning probability of survival ²	Fraction living at of interval	Probability of death stage	Fraction of all deaths the beginning	Fraction of deaths from		Daily
					predation	parasitism	
	Kx	alx	aqx	adx_T	adx1	adx2	Px
Egg (5)	211	1.0000	0.7962	0.7962	0.3697	0.4265	0.7275
Instar I (4)	43	0.2040	0.0698	0.0142	0.0142	0.0000	0.9820
Instar II (7)	40	0.1900	0.2250	0.0427	0.0427	0.0000	0.9642
Instar III (6)	31	0.1470	0.5484	0.0806	0.0806	0.0000	0.8759
Instar IV (6)	14	0.0660	0.6429	0.0427	0.0427	0.0000	0.8423
Instar V (6)	5	0.0230	-	-	-	-	-

[1] – Values inside parenthesis refer to the mean number of days (t_x) spent in each stage based on field data

[2] – Daily ptobability of sutvival obtained as $Px = (1 - q_x)^{(1/tx)}$

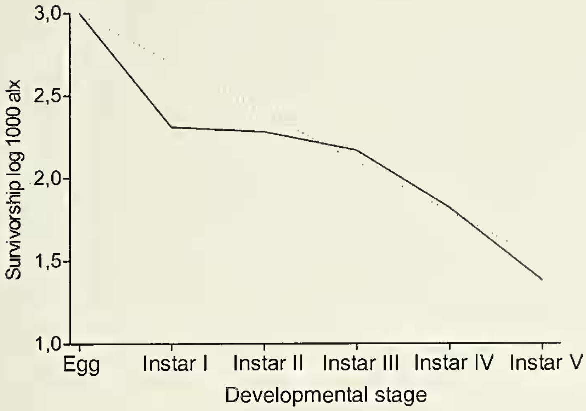

Fig 3. Survivorship curve for immatures of a population of *Hypna clytemnestra* studied for one year at the Reserva de Santa Genebra, Campinas, SP. Dashed line represents a theoretical survivorship curve with constant rate of mortality (Type II).

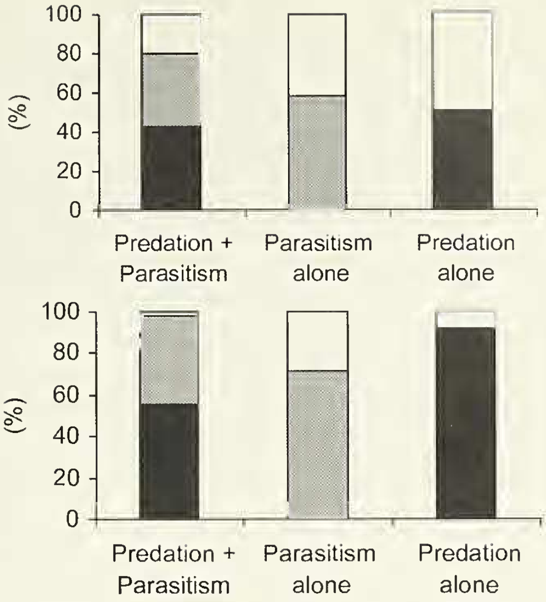

Fig. 4. Intensity of immature mortality inferred from the competing risk analysis applied for eggs alone (A) and for eggs and larval instars combined (B). Left bar shows the original life-table results, middle bar shows the impact of parasitism if predators were not acting and right bar shows the impact of predation in the absence of parasitism.

was eliminated, 49.0% of the eggs would have died from predation as compared to the 36.9% (Fig. 4). When mortality was considered during both egg and all larval instars, elimination of predation would increase parasitism from 42.6% to 71.7%, whereas if predators were acting alone they would be responsible for as much as 91.7% of all deaths, a significant increase over 40.0% (Fig. 4).

DISCUSSION

Hypna clytemnestra immatures showed a marked seasonal fluctuation in abundance during the year, a pattern not followed by the adult stage. The increase in immature number was well synchronized with the increase in rainfall in the wet season. During this time there is an increase in food availability, since a greater number of new leaves, of better nutritional quality are produced by host plants (unpublished data). A likely scenario is that the arrival of summer also results in hotter and longer days and larvae from eggs hatching at this time will develop in a warmer environment and might be feeding on more abundant and better quality leaves. These simultaneous changes in adult and larval environment will act in combination, favoring a faster larval development, shortening generation time and leading to a rapid increase in the butterfly population.

On the other hand, the proximity of the dry season leads to host plant deterioration (i.e. accumulated leaf damage, reduction in water and nitrogen content), which may sometimes result in a reduction in reproductive activity in seasonal habitats (Jones & Rienks 1987; Braby 1995). In addition to that, the increase in immature density in the middle of season may increase the encounter and attack rates on eggs and larvae by parasitoids and predators, which will probably buffer the population increase. The rate of parasitism for fourth instar larvae of *A. ryphea* feeding on the same host plant seemed to increase in response to increase in larval density (Caldas 1996). Other examples of positive density dependence action of parasitoids and predators on herbivorous insects can be found in Stiling (1987, 1988).

In addition to the positive effect mediated by improved host plant quality, a possible negative effect of heavy rainfall on immatures of *Hypna* is the mortality of eggs and larvae by dislodging from leaves (e.g. Blau 1980; Courtney & Duggan 1983). Although such effect was reported by Caldas (1995a) for larvae of the butterfly *A. ryphea* using the same host plant in the area, it was not observed for larvae of *Hypna*.

Young (1981) evaluated the seasonal distribution of two species of Charaxinae in a dry forest of Costa Rica, *Anaea morvus* Boisduvali and *Anaea* (*Zaretis*) *itys* Cramer. For both species, immatures and adults were abundant mainly in the wet season, being rare or even absent during dry season. He detected a low level of larval parasitism and suggested that the seasonal pattern of abundance of *Anaea* populations was a response to a reduction in food quantity and quality. A marked seasonality in immature abundance was also reported for the butterfly *H. ninonia daeta*, which reached high densities at the end of the wet season in a forest patch in southern Brazil (Costa 1991). Host plant abundance and quality was suggested as of primary importance in the dynamics of *H. ninonia daeta*. The correlation between fluctuation of insect abundance and seasonality of rainfall and food availability in tropical habitats has been reported previously by Wolda (1978a, b), but despite the good match between rainfall and population fluctuation, it may be that rainfall pattern is not the main factor causing the increase in immature population of insects (Wolda 1988).

The general mortality pattern described here consists of higher mortality of eggs and late larval instars and high survival of small larvae. However, in a population of *A. ryphea* studied in the same site and feeding on the same host plant, first instar larvae was the stage showing higher mortality during the season, which was attributed mostly to predation and to intense rain (Caldas 1995a, 1996). Nevertheless, in these previous studies mortality of eggs was not quantified. On the other hand, the mortality pattern reported for immatures of *H. ninonia* was similar to that found for *H. clytemnestra*, with more intense mortality suffered by eggs and final instars (Costa 1991).

In temperate regions, population studies including the construction of life tables for immature stages were carried out for some pierid species (e.g. Courtney & Duggan 1983; Cappuccino & Kareiva 1985; review in Courtney 1986). A different mortality pattern was reported for *Anthocharis cardamines* (L.) in Britain, with a relatively low egg mortality and low survival of larvae in early instars (Courtney & Duggan 1983). The extremely low egg parasitism is opposed to the high parasitism rate found for *Hypna*. For the rare *Pieris virginiensis* larval survival was similar to those reported for other more abundant pierids, with less intense mortality during the egg stage and final instars and a higher survival of the initial instars (Courtney 1986). Some other studies showing similar results are those of Courtney (1981) and Hayes (1981) - Pieridae, and Blau (1980) and Rausher (1980) – Papilionidae, while Watanabe (1981) and Feeny et al. (1985) found more constant rates of mortality from eggs to late instars for species of *Papilio*, characterizing a Type II survivorship curve.

The competing risk analyses for *Hypna* revealed that for the egg stage both predation and parasitism are equally important as mortality factors, since the elimination of each one of them leads to a similar compensation (increase) in the intensity of mortality caused by the other. When both eggs and larvae are considered, predators seem to be playing a more important role, since predation would compensate better for the absence of parasitism than vice-versa.

In most published studies mortality was caused by different factors at different stages/instars (see review in Dempster 1984). Eggs can fail to hatch due to apparent infertility, suffer from disease and bacterial attack, be dislodged by rain, die from dissecation or other unknown physiological causes, be parasitized or predated (Baker 1970; Parker 1970; Young & Moffet 1979; Hayes 1981; Watanabe 1981; Courtney & Duggan 1983; Caldas 1995a, 1996). Small larvae can be dislodged by rain, fail to establish in the host plant due to physical or chemical barriers, be parasitized or predated by small arthropods (Baker 1970; Blau 1980; Courtney 1981; Hayes 1981; Watanabe 1981; Courtney & Duggan 1983; Caldas 1995a; Ohsaki & Sato 1994, 1999), while larger larvae tend to be predated by vertebrates, especially birds (e.g. Pollard 1979; Watanabe 1981).

In this study the only cause of mortality detected directly was parasitism of eggs. Parasitized eggs change colour into metalic gray. Predation can only be inferred by the disappearance of eggs and larvae. Despite no observation of a predation event upon *Hypna* immatures, possible invertebrate predators of eggs and small larvae in the area would be ants, spiders and wasps, the first two groups being relatively abundant on *C. floribundus*. Evidence supporting this are observations of ants preying upon eggs (J. M. Queiroz, pers. com.) and of a jumping spider (Salticidae) preying upon a second instar larvae of *A. ryphea*. The direct observations of predation on immatures of *A. ryphea* were probably favored by its higher abundance, and there is no reason to believe that these same predators would not kill immatures of *Hypna* as well. Potential predators of large larvae are wasps and birds.

Attacks by predators, parasitoids and pathogens were the most frequently cited sources of mortality (48%) for immatures of herbivorous insects in 530 published life-tables evaluated by Cornell and Hawkins (1995), which included some studies on Lepidoptera. In a more quantitative analysis of 83 life tables for 78 herbivorous insect species, predators appeared as the dominant natural enemy (as compared to parasitoids and pathogens) of post-egg stages in the tropics and subtropics, whereas parasitoids are dominant in temperate zone (Hawkins et al. 1997). For the population of *H. clytemnestra* investigated, inhabiting a tropical and seasonal environment, natural enemies emerged as the main mortality factors. Considering all stages and instars, predators played a major role, agreeing with the pattern suggested for the tropics in the above review. For the egg stage, death rate was equally due to parasitoids and predators, but the former killed a higher fraction of eggs of *Hypna* than is usual in species of temperate regions.

Regarding habitat use, adults of *Hypna* seem to use equally well both shady, inside forest and gap-like habitats, avoiding to some degree more open habitats such as forest edges. With respect to the low abundance of adults, it is worth noting that I started trapping only in March, and maybe a slight peak in adult abundance in the previous months, namely January and February, would have been detected if I had used traps at that time. On the other hand, despite the decrease of immature numbers in March, the population was still "large". Therefore, I would expect that captures in the following two months would reflect this through the trapping of a higher number of adults, that did not occur. Also interesting was the presence of adults through all the year, even during the drier and colder months, and the low number of individuals trapped in January and February, 2000.

For the rare *Pieris virginiensis* in temperate regions, unfavorable climatic conditions for flying and laying eggs, difficulty in finding the host plant hidden by neighboring vegetation, mortality caused by starvation and predation when locating secondary host plants to complete development, and the inability of adults to cross open fields and colonize new adequate habitats all acted to shape the populations at low densities (Cappuccino & Kareiva 1985). Except for unfavorable climatic conditions, most of the cited factors do not apply to *H. clytemnestra*. Its low abundance, even during the middle of the wet season when individuals are supposed to have been the best environmental conditions, seems to be shaped mainly by the intense mortality suffered by the immature stages due to the action of natural enemies, namely high parasitism and predation upon eggs and predation upon larvae.

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LITERATURE CITED

BAKER, R. R. 1970. Bird predation as a selective pressure on the immature stages of the cabbage butterflies, *Pieris rapae* and *P. brassicae*. Journal of Zoology 162: 43-59.

BLAU, W. S. 1980. The effect of environmental disturbance on a tropical butterfly population. Ecology 61: 1005-1012.

BRABY, M. F. 1995. Reproductive seasonality in tropical satyrine butterflies: strategies for the dry season. Ecological Entomology 20: 5-17.

CALDAS, A. 1994. Biology of *Anaea ryphea* (Nymphalidae) in Campinas, Brazil. Journal of the Lepidopterist's Society 48: 248-257.

CALDAS, A. 1995a. Population ecology of *Anaea ryphea* (Nymphalidae): immatures at Campinas. Brazil. Journal of the Lepidopterist's Society 49: 234-245.

CALDAS, A. 1995b. Mortality of *Anaea ryphea* (Lepidoptera: Nymphalidae) immatures in Panama. Journal of Research on the Lepidoptera 31: 195-204.

Caldas, A. 1996. Intraseasonal variation in a population of *Fountainea ryphea* (Cramer) (Lepidoptera. Nymphalidae). Revista Brasileira de Zoologia 13: 399-404.

Cappuccino, N. 1995. Novel approaches to the study of population dynamics, pp. 3-15. *In*: N. Cappuccino & P. W. Price(eds.), Population dynamics: new approaches and synthesis. Academic Press, San Diego, California.

Cappuccino, N. & P. Kareiva. 1985. Coping with a capricious environment: a population study of a rare pierid butterfly. Ecology 66: 152-161.

Carey, J. R. 1993. Applied demography for biologists with special emphasis to insects. Oxford University Press, New York, NY, 206 pp.

Comstock, W. P. 1961. Butterflies of the American tropics. The genus *Anaea*, Lepidoptera, Nymphalidae. American Museum of Natural History, New York, 214 pp.

Cornell, H. V. & B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. American Naturalist 145: 563-593.

Cornell, H. V., B. A. Hawkins & M. E. Hochberg. 1998. Towards an empirically–based theory of herbivore demography. Ecological Entomology 23: 340-349.

Costa, F. A. P. L. 1991. Sobre a utilização de *Solanum cernuum* Vell. (Solanaceae) como planta hospedeira por *Hypothyris ninonia daeta* Bdv. 1836 (Lepidoptera: Nymphalidae: Ithomiinae). Unpublished M.Sc.Thesis. Universidade Estadual de Campinas, Campinas, SP, Brazil, 218 pp.

Courtney, S. P. 1981. Coevolution of pierid butterflies and their cruciferous foodplants. III. *Anthocharis cardamines* L. survival, development and oviposition on different host plants. Oecologia 51: 81-86.

Courtney, S. P. 1986. The ecology of pierid butterflies: dynamics and interactions. Advances in Ecological Research 15: 51-131.

Courtney, S. P. & A. E. Duggan. 1983. The population biology of the Orange Tip butterfly *Anthocharis cardamines* in Britain. Ecological Entomology 8: 271-281.

Dempster, J. P. 1983. The natural control of populations of butterflies and moths. Biological Review 58: 461-481.

Dempster, J. P. 1984. The natural enemies of butterflies, pp. 9-21. *In*: R. I. Vane-Wright & P. R. Ackery (eds.), The Biology of Butterflies. Symposium of the Royal Entomological Society, Academic Press, London.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22: 283-314.

DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, New Jersey, 325 pp.

Ehrlich, P. R. & L. E. Gilbert. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5: 69-82.

Feeny, P. P., W. S. Blau & P. M. Kareiva. 1985. Larval growth and survivorship of the black swallowtail butterfly in central New York. Ecological Monographs 55: 167-187.

Freitas, A. V. L. 1993. Biology and population dynamics of *Placidula euryanassa*: a relict ithomiine butterfly (Nymphalidae: Ithomiinae). Journal of the Lepidopterist's Society 47: 87-105.

Freitas, A. V. L. 1996. Population biology of *Heterosais edessa* (Nymphalidae) and its associated Atlantic forest Ithomiinae community. Journal of the Lepidopterist's Society 50: 273-289.

Freitas, A. V. L. & R. R. Ramos. 2001. Population biology of *Parides anchises nephalion* (Papilionidae) in a coastal site in Southeast Brazil. Brazilian Journal of Biology 61: 623-630.

Freitas, A. V. L., J. Vasconcellos-Neto, F. Vanini, J. R. Trigo & K. S. Brown jr. 2001. Population studies of *Aeria olena* and *Tithorea harmonia* (Nymphalidae, Ithomiinae) in Southeastern Brazil. Journal of the Lepidopterist's Society 55: 150-157.

Hawkins, B. A., H. V. Cornell & M. E. Hochberg. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. Ecology 78: 2145-2152.

Hayes, J. L. 1981. The population ecology of a natural population of the pierid butterfly *Colias alexandra*. Oecologia 49: 188-200.

Hayes, J. L. 1984. *Colias alexandra*: a model for the study of natural populations of butterflies. Journal of Research on the Lepidoptera 23: 113-124.

Jones, R. E. & J. Rienks. 1987. Reproductive seasonality in the tropical genus *Eurema* (Lepidoptera: Pieridae). Biotropica 19: 7-16.

Morellato, P. C. & H. F. Leitão-Filho. 1995. Ecologia e preservação de uma floresta tropical urbana: reserva de Santa Genebra. Editora da Unicamp, Campinas, SP, 136 pp.

Ohsaki, N. & Y. Sato. 1994. Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. Ecology 75: 59-68.

Ohsaki, N. & Y. Sato. 1999. The role of parasitoids in evolution of habitat and larval food plant preference by three *Pieris* butterflies. Research on Population Ecology 41: 107-119.

Parker, F. D. 1970. Seasonal mortality and survival of *Pieris rapae* (Lepidoptera: Pieridae) in Missouri and the effect of introducing an egg parasite, *Trichogramma evanescens*. Annals of the Entomological Society of America 63: 985-994.

Pollard, E. 1979. Population ecology and change in the range of the white admiral butterfly, *Ladoga camilla* L. in England. Ecological Entomology 4: 61-74.

Price, P. W. 1991. Darwinian methodology and the theory of insect herbivore population dynamics. Annals of the Entomological Society of America 84: 465-473.

Quintero, H. E. 1988. Population dynamics of the butterfly *Heliconius charitonius* L. in Puerto Rico. Caribbean Journal of Science. 24: 155-160.

Ramos, R. R. & A. V. L. Freitas. 1999. Population biology and wing color variation in *Heliconius erato phyllis* (Nymphalidae). Journal of the Lepidopterist's Society 53: 11-21.

Rausher, M. D. 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. Evolution 34: 342-355.

Saalfeld, K. & A. M. Araújo. 1981. Studies on the genetics and ecology of *Heliconius erato* (Lepid.; Nymph.). I. Demography of a natural population. Revista Brasileira de Biologia 41: 855-860.

Stiling, P. 1987. The frequency of density dependence in insect host-parasitoid systems. Ecology 68: 844-856.

Stiling, P. 1988. Density-dependent processes and key factors in insect populations. Journal of Animal Ecology 57: 581-593.

Vanini, F., V. Bonato & A. V. L. Freitas. 2000. Polyphenism and population biology of *Eurema elathea* (Pieridae) in a disturbed environment in tropical Brazil. Journal of the Lepidopterist's Society 53: 159-168.

Vasconcellos-Neto, J. 1980. Dinâmica de populações de Ithomiinae (Lep., Nymphalidae) em Sumaré-SP. Unpublished M.Sc. Thesis. Universidade Estadual de Campinas, Campinas, SP, Brazil, 206 pp.

Walter, H. 1985. Vegetation of the earth. Springer-Verlag, Berlin, Germany, 237 pp.

Watanabe, M. 1981. Population dynamics of the swallowtail butterfly, *Papilio xuthus* L., in a deforested area. Research on Population Ecology 23: 74-93.

Wolda, H. 1978a. Fluctuations in abundance of tropical insects. American Naturalist 112: 1017-1045.

Wolda, H. 1978b. Seasonal fluctuations in rainfall, food and abundance of tropical insects. Journal of Animal Ecology 47: 369-381.

Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics 19: 1-18.

Young, A. M. 1981. Notes on the seasonal distribution of *Anaea* butterflies (Nymphalidae) in tropical dry forests. Acta Oecologica 2: 17-30.

Young, A. M. 1982. Natural history of *Hypna clytemnestra* Cr. (Nymphalidae) in Costa Rica. Journal of the Lepidopterist's Society 36: 310-314.

Young, A. M. & M. W. Moffet. 1979. Studies on the population biology of the tropical butterfly *Mechanitis isthmia* in Costa Rica. American Midland Naturalist 101: 309-319.